

SUN COMPASS ORIENTATION OF PIGEONS UPON DISPLACEMENT NORTH OF THE ARCTIC CIRCLE

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The use of the sun compass by animals poses interesting and thus far unsolved problems when we consider animals which migrate over many degrees of latitude. Drastic changes in the sun's rate of change of azimuth, direction of movement, etc., are encountered as one changes latitude. The general aspects of this problem have been discussed in more detail by Braemer (1960) and in a recent paper in this journal by Schmidt-Koenig (1963).

Birds in particular are known to travel over long distances. Examination of the response of directionally trained birds upon long distance latitudinal displacement may help to answer the relevant questions.

Two experimental series of experiments on sun compass orientation in birds upon large latitudinal displacement have so far been reported. Hoffmann (1959) displaced starlings (*Sturnus vulgaris*) from Wilhelmshaven, Germany, to Abisko, Sweden. Schmidt-Koenig (1963) took homing pigeons from Durham, N. C., to Belem, Brazil, and to Montevideo, Uruguay. The results of another experiment involving large northward translocation of homing pigeons from Durham, N. C., to Barrow, Alaska, will be dealt with in this paper.

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METHODS AND ANIMALS

A description of the semi-automatically operating apparatus for training and testing, the mathematical procedure and the calculation of solar data was given previously (Schmidt-Koenig, 1963). Upon return from the South America experiment (op. cit.) the southward training of pigeons No. 1, 3, 6, and 7 was reinforced at Durham, N. C., in the spring of 1962. In addition, pigeons No. 10 and 14, also offspring of the Wilhelmshaven strain bred at Duke University, were

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newly trained to the east. Pigeons No. 3, 6, and 14 were shipped to Montevideo for another series of transequatorial tests. Unfortunately, Uruguayan officials sacrificed the birds upon arrival. Pigeons No. 1, 7, and 10 remained for the Alaska experiment.

EXPERIMENTS AND RESULTS

The translocation experiment to Alaska was planned to fall around the summer solstice of 1962. On June 7, 1962, the birds were trained for the last time at Durham ($36^{\circ} 00' N$; $78^{\circ} 56' W$). The travel to Barrow, Alaska ($71^{\circ} 10' N$; $150^{\circ} 41' W$), involved a longitudinal time shift of about 5 hours counterclockwise. In order to facilitate the adjustment, experimenter and birds traveled by rail from Durham, N. C., to Seattle, Washington, from June 9, to June 13, 1962. The travel from Seattle to Barrow took another two days of waiting and flying. In Barrow, the birds were housed in their transportation crate in a greenhouse of the Arctic Research Laboratory. They were covered from four hours before midnight to four hours after midnight until June 18, 1962. From then on they were exposed to the permanent Arctic day. The location of the crate in the greenhouse prevented the birds from directly seeing the sun from about two hours before to three hours after midnight.

A site without tall landmarks around it was found just west of the Arctic Research Laboratory. The minimum altitude of the midnight sun at Barrow was 5° . For the tests around midnight, the aluminum palisade of the experimental apparatus was replaced by a double-layer gauze screen. Tests were performed from June 17 through June 29, 1962, with one or two, exceptionally three, sessions per 24 hours. There was no training. The weather was unusually favorable. Only on a few days was no sun shining at all.

It was intended to obtain a score from each bird for every half hour of the 24 hours of the day, but, when the dichotomy of behavior at "night" appeared, more attention was paid to the critical hours around and after 6 p.m. The performance of the birds (No. 10 recalculated as if trained to the south) and the sun azimuth curve for the summer solstice for the experimental and the home location are given in Figure 1. During "day" time the birds allowed by and large for a northern hemisphere sun azimuth. The present method is, however, too insensitive and the total number of scores is too small to tell whether the birds referred to the Barrow or the Durham azimuth. But the approach is sufficiently sensitive to reveal a clear dichotomy of behavior at "night." The birds referred to the sun as if it were moving clockwise (*i.e.*, through north) as well as if it were moving counterclockwise (*i.e.*, through south) at "night" time. The former is demonstrated by the extension of scores along the Barrow sun azimuth curve, the latter by the scores branching off to the upper right in Figure 1.

DISCUSSION

Previously, certain taxa of animals have been found to allow either for a sun moving clockwise at night ("bee pattern") or for a sun moving counterclockwise at night ("*Talitrus* pattern"). Examples of the former are bees (Lindauer, 1957), certain riparian spiders (Papi and Syriämäki, 1963), starlings (Hoffman, 1959),

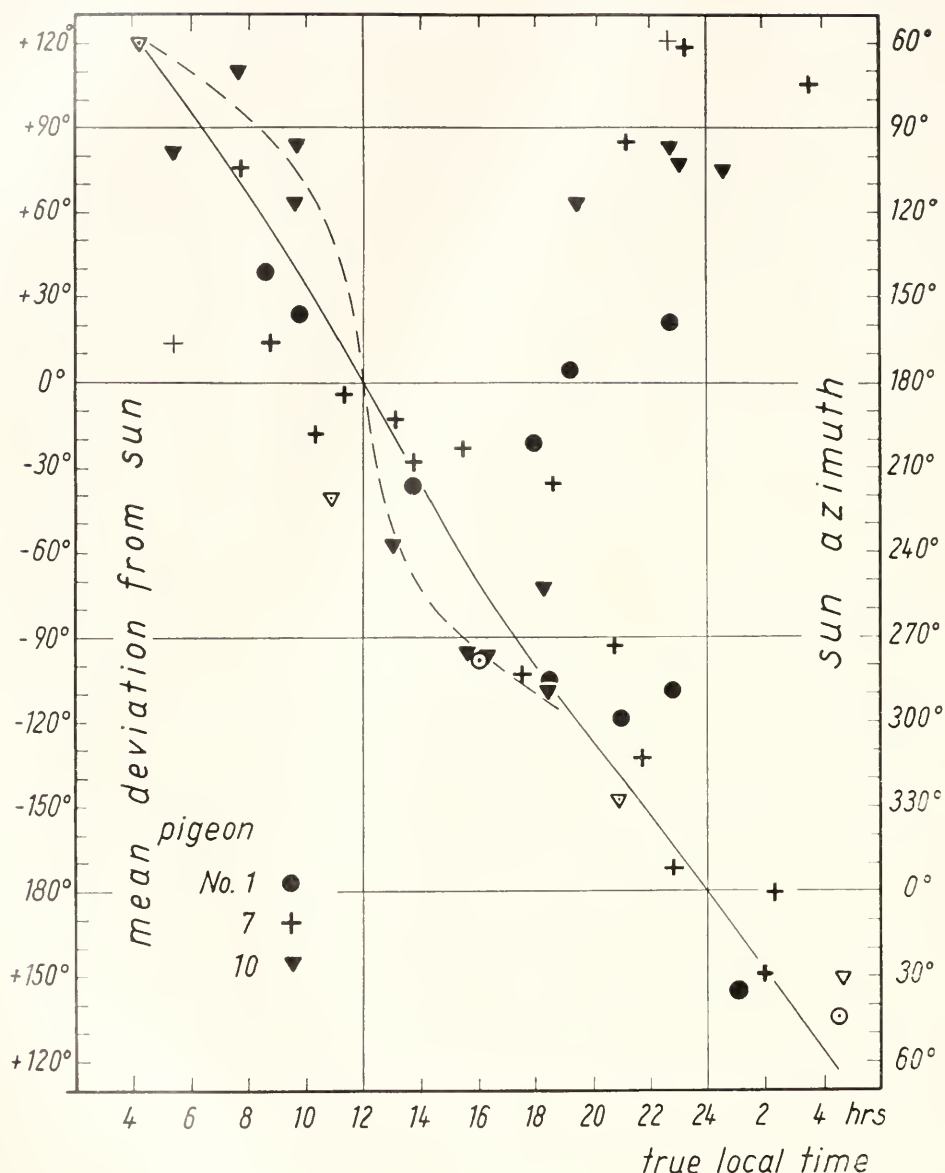


FIGURE 1. The performance of the three pigeons (key inserted at the lower left) at Barrow, Alaska. Each score represents the direction of the mean vector of all unrewarded choices during one examination session performed at the time of day (true local time = TLT) indicated on the abscissa and plotted as angle to the actual sun azimuth position (left coordinate). Black symbols represent 6-20 choices non-random at $p \leq 0.05$ (Rayleigh test), light symbols those random at $p > 0.05$. Open symbols with a central point summarize less than 6 choices. The solid diagonal line gives the sun azimuth at Barrow on June 21, 1962, the dotted line that at Durham, N. C., on the same date. The right coordinate designates true sun azimuth positions.

and fish (Braemer, 1959; 1960). Examples of the latter are a number of arthropods (Pardi, Papi, Birukow and others; see Pardi, 1960, and Birukow, 1960, for references), and pigeons (Schmidt-Koenig, 1961).² Papi and Syriämäki (1963) found two different patterns in different populations of one species of spiders (*Arctosa cinerea*). Finnish populations exhibited the bee pattern, Italian populations showed no definite orientation at night but some tendency for the *Talitrus* pattern. The results given in the present paper demonstrate that individual pigeons may exhibit both the bee pattern and the *Talitrus* pattern.

It is obvious to ask which factors trigger the alternative behavior. At least the data on birds may suggest this to be a function of the day-night conditions the birds are living in. The two pigeons of Schmidt-Koenig (1961) lived in a 12/12 hr. LD cycle (that was shifted to permit tests under the natural sun). Hoffmann's (1959) starlings, which allowed exclusively for a clockwise movement of the sun, were living in the permanent Arctic day for more than five weeks (that they were retrained in the testing area may also be relevant). The pigeons showing both patterns (Fig. 1) lived in the permanent Arctic day at Barrow for only 10 days. This type of behavior may, therefore, perhaps be interpreted as a transition from one pattern to the other. The bee pattern is certainly the only useful pattern. On the other hand, starlings have not yet been tested at "night" when living in an LD cycle and it is not known whether the *Talitrus* pattern can be produced at all.

The two-component theory of the sun compass (Mittelstaedt, 1963) is capable of explaining the alternative behavior even in individuals. The theory predicts the branching-off of the alternative behavior for 18:00 hours. The data from the pigeons (in this paper and in Schmidt-Koenig, 1961) do not seem to be fully consistent with this prediction. The entire branch of the (nocturnal) counter-clockwise pattern does not represent the precise mirror image of the diurnal branch. This mirror image would have to go through 0° (left ordinate) at 24 hours TLT (abscissa), but the scores are displaced to the left of this theoretical line. In other words, the birds bore somewhat farther to the right than expected. This deviation is unexplained. More experiments are clearly needed to establish fully the response of birds to the various experimental and natural conditions.

SUMMARY

1. Three homing pigeons, directionally trained in a semi-automatically operating apparatus at Durham, N. C. (36° 00' N; 78° 56' W), were displaced to Barrow, Alaska (71° 10' N; 150° 41' W), around the summer solstice of 1962.
2. At "night" the birds allowed dichotomously for a clockwise and a counter-clockwise movement of the sun. This is the first indication that individuals may follow the "bee pattern" as well as the "*Talitrus* pattern."

² Fish in the northern hemisphere have been found to follow the bee pattern (Braemer, 1959), while others (of a different genus) on the equator followed the *Talitrus* pattern (Braemer, W., and H. Schwassman, 1963. Vom Rhythmus der Sonnenorientierung am Äquator (bei Fischen). *Ergebn. Biol.*, 26: 253-258).

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